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A New Alligator Lizard from the Panamint Mountains, Inyo County, California

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In the higher mountains of southwestern United States, as in arid regions elsewhere in the world, are isolated species of plants and animals that are unable to exist in the surrounding dry lowlands. They or their ancestors must have dispersed across the intermountain basins at a time when conditions of temperature and humidity were more favorable to them than now. The divergence of many of the isolated organisms from their closest relatives in other areas indicates an evolutionary history antedating man.

During the Pluvial period the Great Basin and parts of the Colorado Desert were well watered. At various times and places there existed lakes, marshes, streams, and a mesic flora and fauna. The present distribution of fresh-water fishes (Hubbs and Miller, 1948) provides convincing evidence for interconnected waterways in the intermountain area. Mesic conditions on the land must have accompanied the expanded water systems, as indicated by botanical evidence and the present distribution of many terrestrial animals. The present ranges of species of ectotherms that are intolerant of high temperatures and dryness are particularly suggestive. Among reptiles the ringneck snakes (*Diadophis*), black-headed snakes (*Tantilla*), and Gilbert's skink (*Eumeces gilberti*) are noteworthy. Each of these is found over a large area in California west of the Sierran crest and on the central plateau of Arizona. Each has one or more relict populations on mountains in the intervening desert area. *Diadophis amabilis* occurs in the Provi-

dence Mountains,¹ San Bernardino County, California, between the main body of the species and *D. regalis* of Arizona, *Tantilla utahensis* in the Panamint and Charleston Mountains, between *Tantilla eiseni* of California and *T. atriceps* of Arizona, and *Eumeces gilberti* in the Panamints, between the main body of the species in California and an isolated population on the Arizona plateau.

Once more the Panamint Range is found to afford sanctuary for a reptile that is intolerant of desert conditions. On October 23, 1954, James McDonald, Jr., found an alligator lizard (*Gerrhonotus*) in Surprise Canyon at an elevation of 4500 feet. Subsequent collecting provided additional specimens, and the present study shows this lizard to be related to *Gerrhonotus multicarinatus* (including its close relatives *paucicarinatus* and *cedrosensis*) and *G. kingi*, yet sufficiently different to be regarded as a new species. We may add, therefore, another example of a reptilian desert isolate suggestive of a former connection between mesic elements in the herpetofauna of Arizona and those of California.

The following abbreviations are used:

A.M.N.H., the American Museum of Natural History

C.H.L., Charles H. Lowe, Jr., private collection

M.V.Z., Museum of Vertebrate Zoology, University of California, Berkeley

R.C.S., Robert C. Stebbins, private collection

U.I.N.H.M., University of Illinois Museum of Natural History, Urbana

U.M.M.Z., University of Michigan Museum of Zoology, Ann Arbor

U.S.N.M., United States National Museum, Washington

***Gerrhonotus panamintinus*, new species**

Figure 1

TYPE: M.V.Z. No. 65410, collected by James McDonald, Jr., October 23, 1954, in Surprise Canyon, at an elevation of 4500 feet, on the west side of the Panamint Mountains, Inyo County, California.

DESCRIPTION OF TYPE: Measurements, in millimeters, after preservation: Snout to vent length, 112.9; tail, 149.7 (70.8 regenerated); head width, 16.5, length (to anterior margin of ear opening), 26.1, greatest depth, 7.6; axilla to groin, 58.2; anterior border of insertion of forelimbs to tip of snout, 39.1; forelimb (from point of limb insertion to outer curve of nail of longest toe), 29.2; hind limb, 37.1; greatest width of tail, 12.3.

¹ I am indebted to Dr. Charles Lowe for this record. The specimen (C.H.L. No. 4061) was collected in May, 1950, at Mitchell's Caverns by Mr. George F. Parker.

SCUTELLATION: Dorsal scale rows, 44–46 (counted, respectively, on right and left sides of midline, from immediately behind ear opening to above posterior margin of the thighs); ventral scale rows, 65 (mental to preanals inclusive); longitudinal dorsal rows, 14; longitudinal ventral rows, 12; limbs without keeled scales except on upper surface of distal segment of hind limbs; number of rows of keeled scales on tail (counted on first whorl from base that contains 20 scales), six; dorsal rows of keeled scales on trunk, 12; head scales, including temporals, all smooth.

COLOR (IN LIFE): Dorsal surface of head light olive gray (Deep Olive-Gray¹), unmarked; no yellow on snout; labials light gray; broad area behind eye purplish gray; anterior edge of ear opening white; side of neck ash gray; iris pale yellow (Sulphur Yellow), with blackish area posteriorly; distal end of tongue light sooty brown; cross bands on body and tail brown (Wood Brown), edged posteriorly with dusky brown; seven complete and one partial band between anterior border of hind limbs and occiput; borders of bands vague; bands dull lavender (Drab-Gray) on sides; interspaces light yellow (between Olive Buff and Deep Olive-Buff); regenerated portion of tail light dusky beige; ground color of upper surfaces of limbs light purplish gray, with touches of tan, most pronounced on hind limbs; front toes dull yellow; hind toes beige; sides of body with sooty brown vertical bars faintly edged posteriorly with white; area of granular scales of lateral fold dull lavender, with large whitish spots of vague outline and composed of groups of white scales; sides of tail dull lavender, with light orange-rust bars of faint outline that are continuous with brown cross bands; under sides of limbs whitish; scales of all ventral surfaces gray (Pale Neutral Gray), edged with whitish; ventral color lightens on throat and chin.

PARATYPES²: Three juveniles, an adult male, and three shed skins (see tables 1 and 2).

Juvenile (M.V.Z. No. 65403, fig. 1B), 53.6 mm. Dorsal surface of head pale grayish beige, grading to beige posteriorly, immediately anterior to first dusky cross band; tip of snout pale yellow; dusky eye stripe with white streak below and behind eye; iris pale yellow, with orange cast (between Pale Ochraceous-Salmon and Light Ochraceous Buff) and with dusky blotch posteriorly; dark cross bands on body blackish, those on tail blackish brown; interspaces orange-beige (Ochraceous-Buff)

¹ Capitalized colors are from Ridgway (1912).

² Descriptions of paratypes are of colors in life.

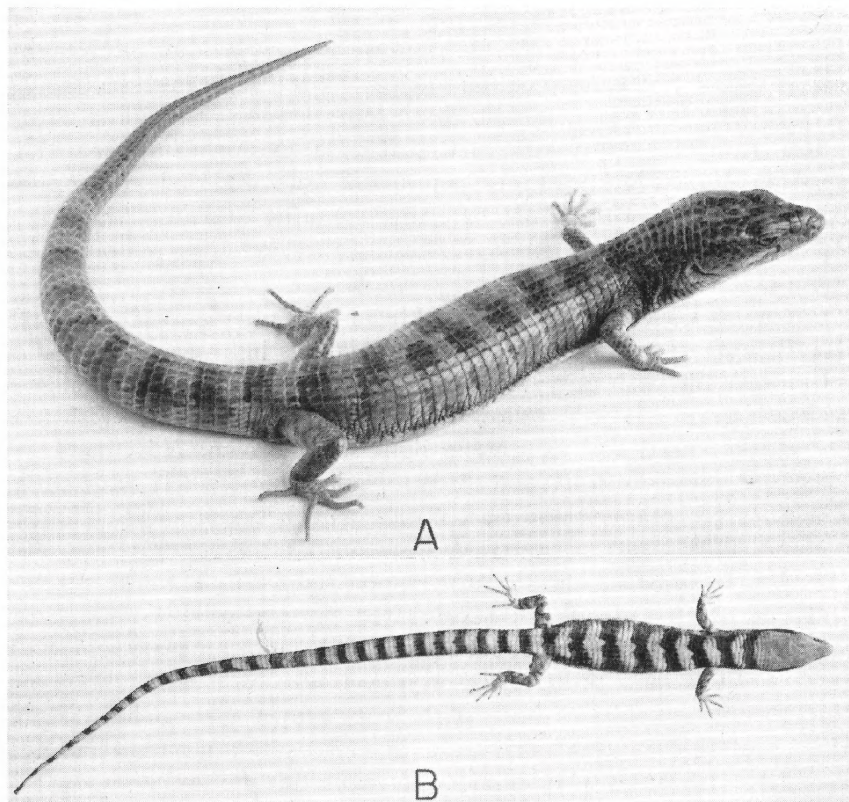


FIG. 1. A. Type of *Gerrhonotus panamintinus*, adult female, M.V.Z. No. 65410, 112.9 mm. in snout to vent length, found by James McDonald, Jr., on October 23, 1954, in Surprise Canyon, 4500 feet, in the Panamint Mountains, Inyo County, California. Note broad cross bands and weak lateral markings as compared with *Gerrhonotus kingi* (fig. 2). The distal end of the tail has been regenerated. Photograph of living animal. B. Juvenile *Gerrhonotus panamintinus*, M.V.Z. No. 65403, 53.6 mm. in snout to vent length, from Limekiln Spring, 3800 feet, Surprise Canyon, Panamint Mountains, Inyo County, California, collected by the author on April 30, 1955. Note contrasting cross bands and lack of melanic pigment on dorsal surface of head.

centrally but dull white laterally; upper surfaces of limbs light and dark banded; ventral surfaces white, with gray blotches that tend to form irregular cross bands on tail; ventral blotching reduced on throat and chest.

Juvenile (M.V.Z. No. 65405), 53.6 mm. Dorsal surface of head light yellowish olive; rostral scale yellow; area immediately around eye dusky but whitish below and dusky patch posterior to eye; iris yellow-

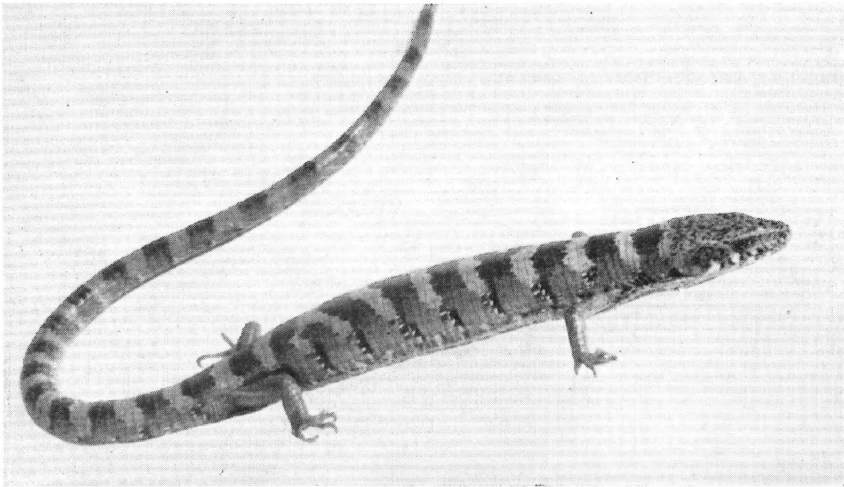


FIG. 2. Live adult *Gerrhonotus kingi* from central Arizona, received through the courtesy of Dr. Charles Lowe, Jr.

ish olive, grading to yellow around pupil; cross bands on body black, lightening to blackish brown on tail; interspaces between bands orange-yellow, grading to white laterally; regenerated portion of tail light gray-brown; feet yellowish, brightest on under surfaces; ventral surfaces of body white with blotches of dusky, which tend to form irregular bands on under side of tail; markings reduced on throat and chest.

Juvenile (M.V.Z. No. 65407), 54.8 mm. Resembles M.V.Z. No. 65405. Adult male (M.V.Z. No. 65409), 118.6 mm. Resembles the type.

DIAGNOSIS: Size of adults large, probably commonly over 100 mm. in snout to vent length; transverse rows of dorsal scales, 44 to 47; number of keeled longitudinal rows of dorsal scales, 10 or 12; scales of temporal region and forelimbs smooth; complete cross bands on body, exclusive of tail, eight or nine; juveniles contrastingly marked with light and dark cross bands; ventral surfaces whitish, with gray spots at middle or sides of scales, forming irregularly arranged blotches; iris pale yellow.

COMPARISONS: *Gerrhonotus panamintinus* appears to be more closely related to *G. multicarinatus* and *G. kingi* than to *G. coeruleus*. Characteristics shared with *multicarinatus* and *kingi* and in which it differs from *coeruleus* are as follows: 1. Although only two adults are available, it appears likely that *panamintinus* averages larger than *coeruleus*. 2. In the individual with intact tail, the tail is close to two times the snout to vent length and contains 122 whorls of scales. In

TABLE 1
MEASUREMENTS (IN MILLIMETERS) OF PARATYPES OF *Gerrhonotus panamintinus*

M.V.Z. No.	Sex	Locality	Date	Snout to Vent	Tail	Width	Head Length	Depth	Axilla to Groin	Fore- limbs	Hind Limbs
65409	♂	Limekiln Spring, 3800 feet	June 23, 1955	118.6	Regen.	19.0	27.0	8.9	62.1	29.0	37.3
65403	?	Limekiln Spring, 3800 feet	April 30, 1955	53.6	104.3 (122 whorls)	8.0	12.6	3.6	28.5	13.6	18.1
65405	?	Brewery Spring, 4800 feet	June 22, 1955	53.6	Regen.	8.3	12.4	3.1	29.4	13.8	18.1
65407	?	Surprise Canyon, 4500 feet	June 22, 1955	54.8	Regen.	8.0	12.5	3.2	29.6	13.7	18.3

TABLE 2
COUNTS OF SCALES AND CROSS BANDS ON THE BODY IN PARATYPES OF *Gerrhonotus panamintinus*

M.V.Z. No.	Dorsal Scale Rows Transverse	Dorsal Scale Rows Longitudinal	Number Keeled	Ventral Scale Rows Transverse	Ventral Scale Rows Longitudinal	Cross Bands Anterior to Sacral Region
65409	46	14	10	67	12	8½
65403	45	14	10	67	12	7
65405	47	14	10	68	12	8
65407	48	14	10	67	12	8
65404 ^a	45	14	10	67	12	?
65406 ^a	46	14	10	68	12	7½
65408 ^a	—	14	10	—	12	8?

^a Shed skins.

TABLE 3

COMPARISONS BETWEEN ADULT *Gerrhonotus multicarinatus*, *G. panamintinus*, AND *G. kingi*

Character	<i>multicarinatus</i> ^a	<i>panamintinus</i>	<i>kingi</i> ^a
Proportions			
Limbs	Long	Long	Short
Scutellation			
Dorsal scale rows			
Transverse	47.2-40.0 (50-39)	45.7 (47-44)	54.6 (60-48)
Longitudinal	14 (occasionally 12; usually 16 in <i>G. paucicarinatus</i>)	14	14 (16 in Mexico?)
Ventral scale rows			
Transverse	66.1-60.5 (70-58)	67 (68-65)	67.4 (74-62)
Longitudinal	12	12	12
Keeling			
Temporals	Upper 2 rows or more	None	None
Dorsal rows	All	10 (rarely 12)	6-8 (weak)
Upper arm	Smooth (<i>scincicauda</i>) to 3 or more	None	None
Lower arm	Smooth to 3	None	None
Tail	8	3-6 (weak)	None
Interocipital	Single (normally)	Single (normally)	Single (normally)
Pigmentation			
Eye color	Yellow	Pale yellow	Orange to pink (rarely gold)
Body bands ^b	10.6 (9-13) [38 individuals]	7.6 (7-8) [7 individuals]	9.4 (8-11) [58 individuals]
Ventral markings	Along middle of longitudinal scale rows, forming longitudinal lines	At middle or sides of scales, forming scattered blotches	Resembles <i>panamintinus</i>
Coloration of young	Longitudinal stripe	Cross bands	Cross bands

^a Scale counts from Fitch (1938).^b Partial bands not counted.

TABLE 4

NUMBER OF CROSS BANDS ON BODY IN INDIVIDUAL SPECIMENS OF *Gerrhonotus*

Number of Cross Bands	<i>panamintinus</i>	<i>kingi</i>	<i>multicarinatus</i>
Seven	1	—	—
+ 1 ^a	2	—	—
Eight	2	2	—
+ 1	2	5	—
+ 2	—	4	—
+ 3	—	—	—
+ 4	—	1	—
Nine	—	8	1
+ 1	—	6	3
+ 2	—	1	—
+ 3	—	1	1
Ten	—	12	4
+ 1	—	9	3
+ 2	—	2	6
+ 3	—	2	—
+ 4	—	—	1
Eleven	—	3	3
+ 1	—	1	7
+ 2	—	1	2
Twelve	—	—	4
+ 1	—	—	1
Thirteen	—	—	2

^a Figures preceded by a plus sign (+) indicate numbers of partial bands in addition to the complete bands indicated above.

coeruleus the tail is often less than twice the snout to vent length, and the number of whorls is usually fewer than 114. 3. As is usually true in *multicarinatus* and *kingi*, there are 14 dorsal scale rows, whereas in *coeruleus* there are usually 16. 4. The scales on the lower sides of the tail are not keeled, whereas they are in adult *coeruleus*. 5. Adults are marked with regular, easily counted cross bands. 6. In *coeruleus* there is considerable melanic pigmentation of the iris, whereas in *panamintinus* the iris is pale yellow without extensive melanic pigment.

Gerrhonotus panamintinus differs from *G. multicarinatus* in having reduced keeling of scales on the head, limbs, and tail, in its generally paler coloration, broad regular cross bands, weak black and white markings on the sides of the body, pale iris, irregular ventral markings, and banded young. From *kingi* it differs in having longer legs, fewer transverse rows of dorsal scales, a greater number of keeled dorsal rows on the body and tail, generally fewer and paler cross bands (fig. 2), absence of prominent dark and light barring on sides, lack of dark and light markings on the labials, and a pale yellow rather than pink iris (see table 3).

There is little overlap between *panamintinus* and *kingi* in number of cross bands on the body and no overlap between *panamintinus* and *multicarinatus* (table 4).

Bands were counted from immediately behind the occiput to a line connecting the anterior border of the thighs. Any band with its posterior margin extending posterior to the groin was excluded. The cross bands and interspaces in *panamintinus* appear to average slightly wider than in *kingi*. The greater number of bands in *kingi* appears to be correlated with proportionately greater body length. The specimens of *multicarinatus* used in the study of banding came from Oregon, central California, and Baja California, and of *kingi*, from Arizona, New Mexico, and Mexico.

The markings of a specimen of *multicarinatus* from Crystal Creek Ranch, 6 miles south of Lucerne Valley (town), San Bernardino County, California, are noteworthy. Although in other respects this individual appears to resemble *multicarinatus* closely, in banding it is much like *panamintinus*. The bands are broad, have nearly even posterior borders, and contrast markedly with the ground color. The closest resemblance to this type of banding seen elsewhere occurs in an individual from Caliente Creek, Kern County, California. Like Crystal Creek this is a semi-arid locality.

Crystal Creek is situated on the precipitous north side of the San Bernardino Mountains facing the Mojave Desert. The *Gerrhonotus* there are probably isolated from the remainder of the species in the San Bernardinos. An isolated population of the salamander *Ensatina eschscholtzi*, a remnant of a formerly widespread type (Stebbins, 1949, pp. 463-467), occurs at the same locality. The habitat is remarkably similar to that of *G. panamintinus*, including a stream with riparian growth of grape tangles and willow clumps and xeric vegetation on the surrounding slopes. Selection in this population of *multicarinatus* has been in the direction of a color pattern comparable to that of

panamintinus. Contrasting patterns are frequently found in nocturnal or crepuscular amphibians and reptiles in arid and semi-arid environments of the southwest. Examples are *Chionactis*, *Chilomeniscus*, *Lampropeltus*, *Rhinocheilus*, *Heloderma*, *Coleonyx*, and *Ensatina*. I have previously commented on the presumed adaptive significance of such patterns (Stebbins, 1949, pp. 493-495).

Gerrhonotus panamintinus differs from *G. cedrosensis* and *G. paucicarinatus*, close relatives of *G. multicarinatus*, in its larger size and pattern of broad pale cross bands, scattered ventral markings, and less contrasting black and white markings on the sides of the body. It differs from *G. liocephalus* in arrangement of the scutellation of the nose and side of the head, reduced keeling, and in lacking contrasting light and dark markings in the cross bands. From members of the *Barisia* and *Abronia* groups (as recognized by Tihen, 1949b) in Mexico and Central America, it differs in the characters mentioned on page 16 as distinguishing these groups of gerrhonotine lizards.

OCCURRENCE: *Gerrhonotus panamintinus* is known only from Surprise Canyon from 3800 to 4800 feet, on the west side of the Panamint Mountains. There are other similar canyons with permanent water and riparian vegetation that provide suitable habitat, and it may be present in other parts of the mountain system, such as in Jail, Hall, and Happy canyons on the west side and Hanaupah and Johnson canyons on the east side of the range. There are springs at high altitude such as Eagle (9200 feet), Tuber (7600 feet), and others unnamed, but it is doubtful if the species occurs at such high elevations. The areas between the water sources, at altitudes where the lizards are likely to occur, are dry, and it seems certain that, as are the Panamint skinks (*Eumeces gilberti*), the alligator lizard is not only completely isolated from other members of the genus, but the Surprise Canyon population could not be connected with populations that might exist in other canyons.

Brief inspection of the physiography and life zones of the region reveals the "montane island" character of the Panamint Range. Physiographically it is one of the westernmost mountain chains in the basin-and-range system of the Great Basin. As with most of the others its long axis is oriented in a north to south direction, and its slopes are cut by numerous deep canyons. The relief is rugged, and there are sharp ridges and much talus, characteristic of geographically youthful topography. Much of the country rock is limestone, marble, and other metamorphics. The mountains rise from an elevation of approximately 1000 feet in Panamint Valley in the west and from below sea level in

Death Valley to the east, to an elevation of 11,049 feet at Telescope Peak. Both of these desert basins were occupied by lakes during the Pluvial period.

In the span of over 10,000 feet in elevation, in a distance measuring some 6 to 10 miles along the east and west slopes of the mountain, life zones range from the Lower Sonoran to Boreal. Vegetation changes from creosote bush and *Atriplex* on the desert flats and lower slopes through pinyon and juniper at intermediate altitudes to limber pine at high elevations. The Upper Sonoran and Boreal zones are completely surrounded by the Lower Sonoran life zone of the Mohave Desert.

The size of the drainage basins, the high altitudes of their upper reaches, and rock structure combine to hold enough moisture in the form of rain and snow to provide many of the canyons with a permanent flow of water. Most of these streams emerge between 4400 to 5600 feet in elevation and run a course of one to several miles. The upper parts of most of the canyons are dry except for scattered springs. The springs and stream courses are the focal points of plant and animal abundance.

Willows, *Baccharis sergiloides*, *Clematis pauciflora* (?), and wild grape tangles make up the main mass of the vegetation. The riparian growth is closely confined to the canyon bottoms. Except in occasional places, it forms a narrow strip averaging about 8 to 20 feet wide, which fingers far down into the arid Lower Sonoran vegetation. Thus one finds scarlet mimulus (*Mimulus cardinalis*) and maidenhair fern (*Adiantum Capillus*) along the stream, growing within a few feet of creosote bush (*Larrea divericata*).

The locality at Limekiln Spring, 3800 feet, where three individuals of *panamintinus* were found, illustrates the habitat (fig. 3). Water issues from the side of the canyon and cascades about 250 feet down a 45-degree slope to the stream in the canyon bottom. The water is clear and cold (16° C.), and the volume of flow was probably over 12 gallons a minute at the time of our visits. The cascade is almost completely concealed by vegetation which fans out from the source to form a large triangular patch that broadly joins the riparian growth below.

The upper part of the cascade is covered by hummocks of *Clematis* which form a basket-work of mixed dead and green branches. Interspersed are smaller hummocks of maidenhair fern. Here and there the water is exposed, and moss-covered rocks and branches with pale beige encrustations of mineral matter can be seen. This encrusting material occurs on objects in the water or in the splash zone of the



FIG. 3. Habitat of *Gerrhonotus panamintinus* at Limekiln Spring, 3800 feet, Surprise Canyon, Panamint Mountains, Inyo County, California. The spring issues from crest of plant-covered slope on right. Vegetation is chiefly willows, wild grape, and *Clematis*.

stream. There are scattered clumps of *Lobelia cardinalis* (?) and near the source of the cascade is a growth of *Phragmites communis* and *Baccharis sergiloides*. Towards the bottom of the slope the *Clematis* gives way to hummocks of wild grape (*Vitis Girdiana*). The interiors of the grape tangles contain leafless interlocking branches and receive little light when the vines are in leaf. Water can be seen moving across the ground in a sheet in some places beneath the vines. Willows predominate where the cascade reaches the main stream. Beneath them is a layer of dead leaves, sometimes over a foot thick. *Mimulus cardinalis*, *M. guttatus*, and *Stachys albens* (?) grow in the vicinity of the stream, and *Epipactis gigantea* and *Juncus xiphioides* are found in and near the stream.

There is a sharp border to the stream-side vegetation. Beyond it, on exposed talus and fissured rock, are creosote bushes (*Larrea divericata*), cactus, and other desert-adapted plants. In areas near the mesic growth, where the water table is near the surface, are *Datura meteloides* and *Eriogonum fasciculatum*, and bordering and sometimes within the

grape and clematis tangle are *Atriplex canescens* and the mat-forming *Artemisia Ludoviciana*.

Other plants found in the drier rocky areas are *Stephanomeria pauciflora*, *Brickellia Knappiana*, *Senecio Douglasii*, *Viguiera reticulata*, *Euphorbia incisa*, *Mirabilis Bigelovii*, *Sphaeralcea ambigua*, and *Pentstemon fruticiformis*.

The canyon walls show evidence of high water and changes in the position and level of the stream bed, indicating periods of torrential flow characteristic of streams in the arid southwest. During such flood periods the more sedentary animal populations in the canyon bottom must be in large measure swept away. Repopulation occurs chiefly from refuges such as Limekiln Spring that extend above flood levels.

All along the stream course are great quantities of water-worn boulders, gravel, and sand, and recently dislodged, unworn, angular rocks of the talus slides. The myriads of hiding places provided by these slides make the collecting of rock-inhabiting lizards extremely difficult. The rocks are ash white, tan, rust, and pale blue-gray, colors present in the color scheme of the alligator lizards.

Many tons of rocks were moved in obtaining specimens. Several times we saw alligator lizards that escaped because the rock could not be moved fast enough. We set funnel traps and Museum Special snap-traps baited with live grasshoppers but caught only *Cnemidophorus tigris*. Perhaps the best method for future collecting would be to sit quietly beneath the willows and to listen for rustling sounds made by foraging lizards. A number of skinks (shot with heavy rubber bands) were procured this way.

In view of the great difficulty in finding individuals of *G. panamintinus*, details concerning the capture of each specimen are presented (see table 1 for localities and dates of collection).

TYPE SPECIMEN: I quote with slight modification from a letter received November 23, 1954, from James McDonald, Jr.: "[The lizard] was about twenty feet from the stream and was lying in the open. There was algae and . . . water cress in the water and willows and sage brush along the creek. The floor of the canyon was of boulders and gravel. . . . the air temperature had been about 75° F. It was a bright day. We found [the lizard] about 4:30 P.M. when the temperature had dropped quickly to about 60° F. due to a coming storm. The lizard was slow and easily caught."

JUVENILE (M.V.Z. No. 65403): Caught among talus at the base of a cliff about 50 feet from the road at the north border of the willow clump, below the source of the spring. The rocks were covered with

3 to 4 inches of duff, chiefly of grape twigs and willow leaves. The lizard was at a depth of about 3 inches among the rocks and dry yellow soil. The soil at the collection site was 14° C. at 11:15 A.M.; the temperature of the air ½ inch above the ground in the shade was 15° C. The site was several feet higher than, and 40 feet north of, the stream. Branches of willows extended almost to the cliff face, and *Clematis* and other plants grew in niches in the rocks. The entire area, although south-facing, was well shaded. A young *Xantusia vigilis* and a night snake (*Hypsiglena torquata*) were found within a few feet of the alligator lizard.

JUVENILE (M.V.Z. No. 65405): Caught under a large angular rock (2 by 1½ feet by 1 foot) at the source of the spring. The lizard rested on moist soil and small rocks, beneath which trickled water from the spring, at a depth below the surface of 3 or 4 inches. The water issued from the base of a 40-foot, north-facing cliff, from beneath talus at its base. The site was about 3 feet from the main stream, here 5 feet wide and about 10 inches deep. The area received sunlight from 10:00 A.M. to 5:00 P.M. A clump of willows and the cliff blocked the morning sun. Beneath the willows was an extensive accumulation of leaves and dead branches.

The lizard was placed on the ground next to the rock. On a background of buff-colored soil, whitish rocks, and dead willow twigs, it was difficult to see. The light cross bands on the body, in width and color, closely matched many of the twigs, and the black bands matched the shadows. It seems likely that this coloration functions in concealment.

Temperatures taken at the collection site were as follows: water of stream, 16.5° C., air 1 inch above dry ground, 19.5° C., and soil where the lizard was found, 16.5° C. at 5:50 A.M.

JUVENILE (M.V.Z. No. 65407): Caught on the steep north-facing slope (65°) of the stream bank, on a substratum of stabilized alluvium exposed by the stream. The site was about 4 feet above water level in an area well shaded by willows (canopy 25%). Above the alluvium was a high cliff. The lizard was discovered in a mat of *Artemisia Ludoviciana*. It had evidently been resting on the dry soil beneath the vegetation and took refuge among the branches when disturbed. The air temperature at the collection site was 24.3° C.; water of the stream, 16.7° C.; air temperature 20 feet from the stream, ½ inch above the dry soil of the road surface, was 31.4° C. (bulb shaded) at 9:55 A.M.

ADULT MALE (M.V.Z. No. 65409): Caught beneath the willows near the collection site of M.V.Z. No. 65403, found by John Burns about

9 A.M. The day before, the willow duff had been excavated over an area 25 feet in circumference. The site was about 20 feet from the stream. The lizard was seen crawling across the churned-up leaf litter.

It is evident from these observations and the discovery of shed skins that *G. panamintinus* is closely restricted to the vicinity of water. Exploration of dry areas yielded no specimens. The greatest distance from water at which a specimen was found was 30 feet. All sites of capture were well shaded, and there was damp soil at or within a few feet of the place of capture.

Although we found no alligator lizards in trees or bushes despite intensive search, the long tail of this species and the behavior of the type specimen in captivity suggest that the lizard is a good climber. The numerous tangles of vines, willow branches, and other growth provide many aerial pathways.

Although situated in an arid region, the habitat is similar to that of *G. kingi* and *G. multicarinatus* with respect to character of the vegetation, substratum, temperature, and moisture conditions.

BEHAVIOR: The type specimen was kept in captivity for over a year. At intervals during this time live individuals of *G. multicarinatus* and *G. kingi* were also under observation. The behavior of the three species was similar. No obvious differences were noted in the method of capturing prey and eating, use of the tail in climbing, and the position assumed when at rest. All three species displayed the habit of resting beneath objects at night, with the tail beside or on top of the head.

The structure, pigmentation, and geographic location of *panamintinus* suggest that it may be a remnant of a widespread prototype from which *kingi* and *multicarinatus*, and its close relatives *paucicarinatus* and *cedrosensis*, were derived. Most of its characteristics fall within the range of variation of these species. However, its isolation and its unique combination of characteristics (long legs and pale yellow eyes associated with smooth scales and broad cross bands) along with features peculiar to itself (ventral markings and pale coloration) warrant its recognition as a distinct species.

REVIEW OF PROPOSED GENERA OF GERRHONOTINE LIZARDS

In an effort to determine the proper taxonomic allocation of the Panamint alligator lizard, a survey was made of the members of the "gerrhonotine" group of lizards of the family Anguidae, as recognized by Tihen (1949b). Although not an exhaustive survey, this study has uncovered some new information which leads me to comment on

systematic relationships within this group of lizards. Tihen (1949b) includes in the gerrhonotine group all Recent anguids with four well-developed limbs and a lateral fold and recognizes five genera (*Abronia*, *Barisia*, *Coloptychon*, *Elgaria*, and *Gerrhonotus*) distributed from British Columbia to Panamá. As a basis for the discussion to follow, these genera may be briefly characterized, essentially as defined by him. In a few instances I add some additional information not presented in his paper.

ABRONIA

A homogeneous group with depressed and widened skull, poorly developed pterygoid teeth, otic and occipital elements fused into a single bone (a unique feature among Recent gerrhonotines), reduced lateral folds, and absence or reduction of the granular scales on the sides of the neck. Although a number of the species are known only from the type specimens, and their habits are unknown, others are known to be arboreal. The presence of long limbs and the frequent occurrence of green coloration in the group suggest that arboreal habits may be common.

These lizards have a disjunct distribution from southern Tamaulipas to Guatemala and include the following 10 species: *aurita*, *bogerti*, *deppi*, *fimbriata*, *fuscolabialis*, *matudai*, *oaxacae*, *ochoterenai*, *taeniata*, and *vasconcelosi*. All appear to be mountain forms, although the locality for *oaxacae* is at an elevation of 300 feet. It perhaps came from a higher altitude near by. *Abronia taeniata* is known to be ovoviviparous (Werler, 1951, p. 41), and it is probable that *A. graminea* also gives birth to its young (Tihen, personal communication). I follow Martin (1955) in recognizing *graminea* as a species.

BARISIA

A variable group with the skull not widened or depressed, the exoccipitals and otic elements fused but the basioccipitals and supraoccipitals independent, moderately to well-developed lateral folds, and the sides of the neck finely granular. The dorsal color is black to brown, or occasionally olive, and there is a strong tendency towards a broad longitudinal stripe. These lizards are terrestrial.

The group ranges from northern Panamá to Chihuahua, Mexico, and includes the following species: *antauges*, *gadovi*, *imbricata*, *levicolis*, *modesta*, *monticola*, *moreleti*, *rudicollis*, and *viridiflava*. As are the abronias, these are mountain forms distributed mostly at high elevations in a disjunct pattern.

ELGARIA

In the scutellation of the lateral folds and neck and lack of flattening and widening of the skull, this genus resembles *Barisia*. It differs from the latter in having well-developed pterygoid teeth and in lacking anterior internasals.

As is *Barisia*, these lizards are terrestrial. The ground color is brown, olive, or grayish. In the species *coerulea* there is a tendency towards a dorsal stripe, but in the other species the pattern consists primarily of dark brown cross bands on a lighter ground color.

The group is represented by five species (*coerulea*, *kingi*, *multicarinata*, *cedrosensis*, and *paucicarinata*) which range from the tip of Baja California and Chihuahua to British Columbia.

GERRHONOTUS

This genus contains only the species *liocephalus*. In many respects this lizard resembles species of the genus *Elgaria*, but it has anterior internasals, apparently always a postrostral, and the suboculars never reach the lowest primary temporal. In the lack of a contact between the prefrontal and nasal, it differs from both *Barisia* and *Elgaria*.

It is a terrestrial species ranging from Chiapas, where it reaches an altitude of over 10,000 feet on Cerro Malé, to central Texas. According to Hobart Smith (personal communication) it is found mostly above 4000 feet in Mexico, although it may occur as low as 1500 feet in central Veracruz.

COLOPTYCHON

There is only one little-known species (*rhombofer*) in this genus, based on what may be an immature specimen from Chiriquí, Panamá. It is distinguished from the *Barisia-Elgaria-Gerrhonotus* complex by differences in head scalation, in weak development of the lateral folds, and in having only 10 ventral scale rows (occasionally true in *Barisia gadovi*). Its habits are unknown.

DISCUSSION

Study of the literature and specimens in collections (see Acknowledgments), along with familiarity in the field with *multicarinatus*, *kingi*, and *coeruleus*, leads me to comment on the genera *Barisia*, *Elgaria*, and *Gerrhonotus* as recognized by Tihen. *Coloptychon* (although poorly known) and the arboreal group *Abronia* seem to stand apart from these genera and are not included in my analysis. For purposes of discussion I use Tihen's taxonomy.



FIG. 4. Habitat of *Gerrhonotus imbricatus* near timber line on north slope of Popocatepetl, 11,000 feet, Mexico. Several individuals, including a female with young ready for birth, were collected by Seth Benson on May 3 and 4, 1940, in bunch grass in foreground.

OVOVIVIPAROUS ALLIGATOR LIZARDS

Although Tihen (1949b, p. 252) had evidence that *Barisia moreleti* was ovoviviparous, he had what he regarded as contrary evidence for the species *imbricata* and *gadovi*. Specimens in the Museum of Vertebrate Zoology of the University of California, however, indicate the presence of ovoviviparity in both *imbricata* and *gadovi*.

An adult female *gadovi* (M.V.Z. No. 57174), collected April 28, 1950, by William Riemer, 3 miles west of Omilteme, 8200 feet, Guerrero, Mexico, contains five fetuses at nearly full term. A female *imbricata* (M.V.Z. No. 36715), obtained by Seth Benson, May 4, 1940, in bunch grass on the north slope of Popocatepetl, 11,000 feet, Mexico (fig. 4), contains five young ready for birth.

The breeding habits of *viridiflava*, *antagues*, *modesta*, and *rudicollis* are unknown. Specimens of *viridiflava* in the University of Illinois

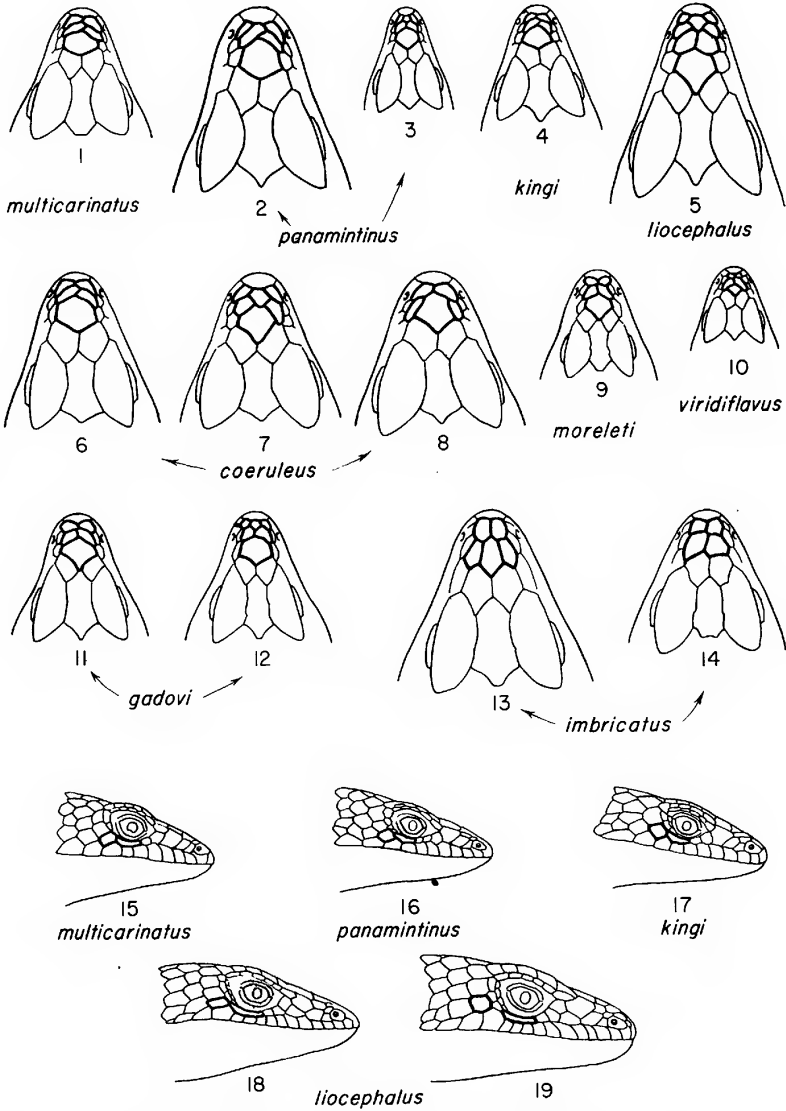


FIG. 5. Variation in scutellation of the head in the subgenera *Gerrhonotus* (Nos. 1 to 5 and 15 to 19) and *Barisia* (Nos. 6 to 14). Drawings based on following specimens: 1, M.V.Z. No. 33642; 2, M.V.Z. No. 65409; 3, M.V.Z. No. 65403; 4, R.C.S. No. 7965; 5, U.S.N.M. No. 58665; 6, M.V.Z. No. 56858; 7, M.V.Z. No. 56861; 8, M.V.Z. No. 51276; 9, U.M.M.Z. No. 100487; 10, U.I.N.H.M. No. 19504; 11, M.V.Z. No. 57175; 12, A.M.N.H. No. 72536; 13, A.M.N.H. No. 1945; 14, A.M.N.H. No. 71663; 15, M.V.Z. no number; 16, M.V.Z. No. 65410; 17, M.V.Z. no number; 18, U.S.N.M. No. 12097; 19, U.S.N.M. No. 12245.

Museum of Natural History have large ovarian eggs, but none was found with embryos. On the basis of its intermediate geographic position between *gadovi* and *moreleti* and its similarity to them in structure and pigmentation, it seems likely that it will prove to have similar reproductive habits. Few specimens of *rudicollis* are available, and as far as I know *antauges* and *modesta* are still known only from the types.

The only other alligator lizard in the *Barisia-Elgaria-Gerrhonotus* groups (as recognized by Tihen, 1949b) that is known to be ovoviviparous is *Elgaria coerulea*. In Tihen's arrangement it is associated with *multicarinata*, an oviparous species. In view of the widespread occurrence of ovoviviparity in the barisias, I have explored the possibility that *coerulea* may belong with them.

I can find no characters in which *coerulea* differs clearly from the barisias when all forms of that group are taken into account. There is overlap in both the character of the scutellation (see fig. 5) in the nasal region and the character of the pterygoid teeth. Specimens of *Barisia gadovi* closely match some *coerulea* in arrangement of the nasal scales (fig. 5).

Both *Barisia gadovi* and *B. viridiflava* are flattened, a feature shared by *Elgaria coerulea palmeri* of the Sierra of California, and *gadovi* has keeling well down on the sides of the tail, as in *coerulea*. In contrast *Elgaria multicarinata* has keeling confined to the upper sides of the tail. One of four *coerulea* skulls available to me lacks pterygoid teeth, and a skull of *Barisia imbricata* has teeth as well developed as those of *coerulea*. The maxillae may or may not be in contact with the frontal as in the barisias. Unfortunately, few skulls of alligator lizards are available.

The similarity in pigmentation between *coerulea* and species of the *Barisia* group (especially *Barisia gadovi*) is close, including the facial markings and configuration of the broad dorsal stripe and its associated pattern. A stripe is present in *coerulea* young and in young barisias, but is absent in the other alligator lizards under consideration except young *multicarinata*. Except for specimens of *multicarinata* from Anacapa Island off the coast of southern California, I know of no other adult members of species in Tihen's genera *Gerrhonotus* and *Elgaria* that have a dorsal stripe.

Although the species *coerulea* and *multicarinata* overlap both in altitude and latitude, and in some places occur in the same area, they show differences in habitat. *Coerulea* prefers moist, relatively cool

situations and ranges farther north and to higher altitudes than *multicarinata*.

In the Berkeley Hills, where the two species are found together, *multicarinata* is widespread, whereas *coerulea* has been found at only a few localities, generally the cooler north slopes where humidity is high. *Multicarinata* is clearly more tolerant of dryness and heat and, particularly in the southern part of its range, tends to be crepuscular and nocturnal. The occurrence of *coerulea* at high altitude and latitude and in humid coastal areas uninhabited by *multicarinata* is probably made possible, in part at least, by its mode of reproduction. It thus appears to be the ecological counterpart of members of the *Barisia* group of Mexico and Central America which resemble it in breeding habits and habitat.

In view of the variation in reproduction in other lizard genera, such as *Sceloporus* and *Phrynosoma*, one should hesitate to use breeding behavior in setting generic or even subgeneric boundaries, but in this instance there is support on other grounds.

In pigmentation, breeding habits, and habitat, *coerulea* appears to me to be closer to members of Tihen's *Barisia* group than to the *Elgaria* group. As there appears to be no clear structural basis for separation of *coerulea* from the *barisias*, I would align it with them on the basis of its pigmentation, habitat, and breeding habits.

OVIPAROUS ALLIGATOR LIZARDS

In view of the presence of the two ecological types *coerulea* and *multicarinata* in western United States, which differ not only morphologically but in habitat and breeding habits, the ecological relationship between members of the *Barisia* group and *Gerrhonotus liocephalus* has been investigated. The species *liocephalus* is similar in structure and pigmentation to *multicarinata* and *kingi*, as brought out by Tihen (1949b).

As is *multicarinata*, *liocephalus* is oviparous, but it has young that are cross-banded (Werler, 1951). Evidence for oviparity comes from the extremes of the range, from Texas (Flury, 1949; Werler, 1951) and Oaxaca (M.V.Z. No. 10323). The latter specimen contains eggs with well-developed shells. In the cross banding of the young, the species resembles *kingi* and *panamintinus*. In contrast, young *E. multicarinata* have a broad longitudinal dorsal stripe. Although the snout is more elongate and there are differences in head scalation (fig. 5) and arrangement of certain of the skull elements, the points of similarity

with *multicarinata* and *kingi*, in my opinion, outweigh these differences. The differences do not seem to be of sufficient magnitude to warrant treatment of *liocephalus* as the representative of a monotypic genus.

The distribution of *liocephalus* in central and southern Mexico, in general, follows that of the *Barisia* group, but *liocephalus* does not reach such high altitudes. Edward Taylor (in correspondence) informs me he doubts if he has taken any *liocephalus* in Mexico above 8000 feet. Although I have had no field experience with this species, I would expect, on the basis of its distribution and breeding habits, that it is more tolerant of heat and dryness than are the barisias. In this connection it should be pointed out that *liocephalus* is not known south of Chiapas, whereas the barisias range to Panamá. Perhaps with further collecting it will be found farther south, but possibly increasing humidity at lower and intermediate elevations and inadequate heat for the development of the eggs of an oviparous alligator lizard at the drier higher altitudes are responsible for its exclusion from these more southerly areas.

In the north *liocephalus* ranges into northern Coahuila, southern Chihuahua, and central and western Texas, at lower altitudes well beyond the barisias, which may be stopped by increasing aridity. Thus the parallel with the *coerulea-multicarinata* relationship in the Pacific northwest seems to hold.

Again, a combination of factors, ecological and morphological, suggests the desirability of realignment of species, and I propose that *liocephalus* be associated with *multicarinatus*, *paucicarinatus*, *cedrosensis*, and *kingi* in the *Gerrhonotus* group, thereby eliminating the monotypic generic arrangement and abolishing use of the name *Elgaria* which is displaced by the priority of *Gerrhonotus*. The species *paucicarinatus*, *cedrosensis*, and *panamintinus* are included on morphological grounds. Their breeding habits are unknown. Mr. William Woodin informs me that a captive female *kingi* from Paul Spur, Cochise County, Arizona, laid 15 eggs on June 5, 1957. To my knowledge this is the first evidence that *kingi* is oviparous.

There is considerable overlap in characters among the species of gerrhonotine lizards. This is particularly evident in the scutellation of the head. In figure 5 note the over-all variation and also the overlap in scale arrangement between species of the two subgeneric groups as recognized below in text (Nos. 3 and 12, and 1 and 6; or 1 and 11, for example). Variation in *coeruleus* bridges both groups (Nos. 1 and 6, and 6 and 11; or 7 and 3, and 7 and 12). In all diagrams, the scales

between the rostral and prefrontals are shown in heavy outline. *Imbricatus* of the *Barisia* group and *liocephalus* of the *Gerrhonotus* group show the greatest differences from the other members of their group. The pattern in *imbricatus* (No. 13), however, is paralleled by *coeruleus* (No. 8), although the scale proportions are greatly different.

Numbers 15 to 17 in figure 5 represent species of the subgenus *Gerrhonotus* that show contact between the suboculars and lowest primary temporal (scales with heavy outline). *Liocephalus* (No. 19) only rarely shows such contact (No. 18).

At the present level of study it is my feeling that little is to be gained by the recognition of more than three genera. Perhaps when a more complete picture is available, the question of generic treatment should be reopened. I propose, therefore, the following taxonomic arrangement for the gerrhonotine group of anigid lizards:

Genus *Gerrhonotus*

Subgenus *Gerrhonotus*

kingi

panamintinus

multicarinatus

cedrosensis

paucicarinatus

liocephalus

Subgenus *Barisia*

antauges

coeruleus

gadovi

imbricatus (*levicollis* regarded as a subspecies)

modestus

monticolus

moreleti

rudicollis

viridiflavus

Genus *Abronia*

Genus *Coloptychon*

The subgenera *Barisia* and *Gerrhonotus* thus consist of two groups of mostly allopatric species, the members of which are similar in structure, breeding habits (so far as known), and ecology, ranging in a disjunct pattern from Central America to the Pacific northwest (fig. 6).

The two subgeneric groups converge in coloration through the forms *coeruleus* and *multicarinatus*. The young of these species are similar in pigmentation; both have a broad longitudinal stripe. The chief difference in coloration lies in the position of the dark blotches

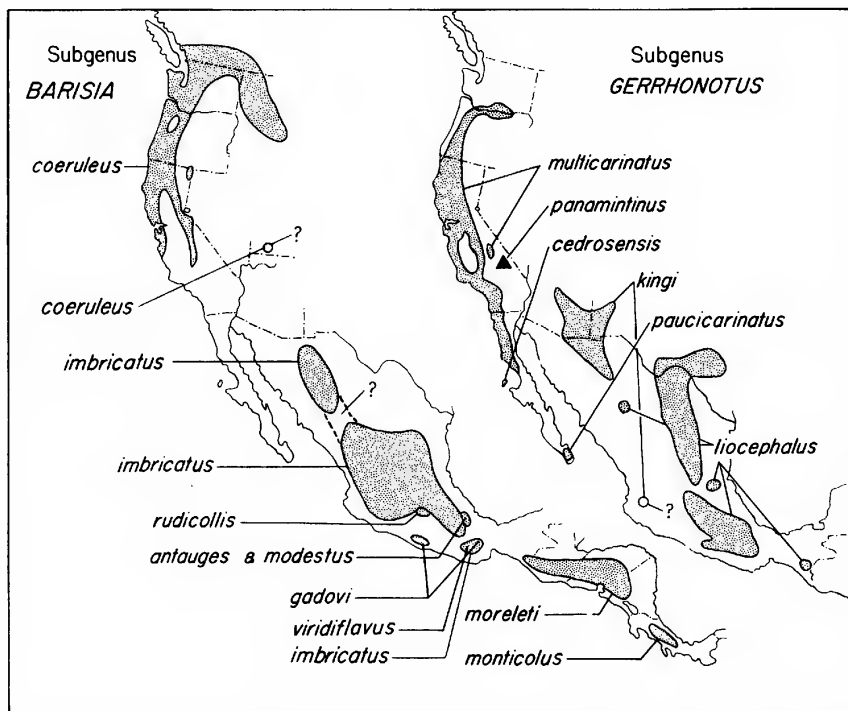


FIG. 6. Distribution of species of the subgenera of gerrhonotine alligator lizards *Barisia* and *Gerrhonotus*. Note the allopatric ranges of the species within each subgeneric group. In the subgenus *Barisia*, the species *Gerrhonotus coeruleus*, *imbricatus*, *gadovi*, and *moreleti* are known to be ovoviviparous. In the subgenus *Gerrhonotus*, *multicarinatus*, *kingi*, and *liocephalus* are known to be oviparous. Questioned localities for *coeruleus* and *kingi* require confirmation.

on the ventral scales. These commonly form longitudinal rows at the middle of the scale rows in *multicarinatus* and between them in *coeruleus*. Other than eye color, there appear to be no other clear-cut color differences. In the Berkeley Hills and elsewhere in coastal areas of California the color markings of the adults also show similarity. The cross bands in some *multicarinatus* are often irregular, suggestive of the markings of *coeruleus*. A specimen (M.V.Z. No. 28329) from West Anacapa Island, Santa Barbara County, California, is especially noteworthy. It lacks cross bands and has instead a variegated dorsal pattern. The melanin pigment on the ventral surfaces tends to be concentrated between the scale rows. In scutellation, however, the specimen resembles *multicarinatus*. Other individuals from the island are more nearly like *multicarinatus* in coloration.

Eggs of *Gerrhonotus multicarinatus* laid in captivity may have embryos at the limb bud stage. The embryo and its membranes occupy perhaps as much as one-tenth to one-twelfth of the total volume of the egg; thus one observes a step in the direction of ovoviviparity. Whether this tendency holds in *liocephalus* or other oviparous species is not known.

I do not know how to interpret these points of similarity. Do they indicate a closer relationship between *coeruleus* and *multicarinatus* than between *coeruleus* and *kingi* or *coeruleus* and *liocephalus*? It appears that the former is the case, although one must also take into account the possibility of convergent evolution. This similarity lends support to the view that the two groups should be accorded no higher taxonomic rank than subgenera.

SPECIMENS EXAMINED

The following material was available for study:

coeruleus, over 200
gadovi, 87
imbricatus, 186
kingi, 70
liocephalus, 71
moreleti, 107
multicarinatus, over 300
panamintinus, 5
paucicarinatus, 3
viridiflavus, 20

ACKNOWLEDGMENTS

Credit for the discovery of *Gerrhonotus panamintinus* goes to James McDonald, Jr., who collected the type specimen, and Mr. Darwin Tieman who, recognizing the scientific value of the lizard, sent it alive to the Museum of Vertebrate Zoology, University of California. At the time of the discovery James was nine years old. Had it not been for his alertness and interest in reptiles, many years might have elapsed before there was scientific recognition of this species. For a youngster his age, he provided an unusual amount of detailed information on locality, habitat, and weather conditions. Subsequently James, his sister Christie, and their parents, Mr. and Mrs. James McDonald, Sr., aided me with field work which resulted in the procurement of additional specimens. In addition they provided my students and me with companionship and a comfortable way station at their home on our

trips to the Panamint area. I wish to express my gratitude to the McDonald family.

In view of the resemblance of *Gerrhonotus panamintinus* to *G. kingi* of Arizona, it was essential to procure living individuals of *kingi* and to see that species in its natural environment. The American Museum of Natural History provided me with this opportunity. I had the good fortune to be one of the guest scientists at the Museum's Southwestern Research Station in the Chiricahua Mountains during the summer of 1956. I wish particularly to thank Dr. Mont A. Cazier, Director of the Station, for his help in obtaining specimens and for his friendly interest in all phases of the work there. With the help of other station personnel, including some of the visiting scientists, a large sample of these secretive lizards was obtained.

A number of institutions and individuals lent or gave me specimens of alligator lizards: Mr. Charles M. Bogert (the American Museum of Natural History), Dr. Norman Hartweg (University of Michigan Museum of Zoology), Dr. Edward Taylor (University of Kansas), Dr. Hobart Smith (University of Illinois Museum of Natural History), Drs. Remington Kellogg and Doris Cochran (United States National Museum), Dr. Howard Gloyd (Chicago Academy of Sciences), Dr. Charles Lowe, Jr. (University of Arizona), Dr. Arthur Loveridge (Museum of Comparative Zoölogy, Harvard College), and Dr. Fred Shannon.

Dr. Charles Lowe, Jr., and Mr. William Woodin, III, supplied me with live *G. kingi*. Dr. Joe Tihen and Mr. Eugene Volz read the manuscript and offered helpful suggestions.

Mr. Dick Thompson permitted us to hunt alligator lizards on his property in Surprise Canyon, and I am particularly grateful for this courtesy.

I also wish to thank members of the staff of the University of California herbarium for the identification of plant samples obtained in Surprise Canyon, and Messrs. James Anderson, John Burns, Richard Russell, Fred Turner, and Eugene Volz and his parents, for help in collecting.

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